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Original article

Wildfire changes the spatial pattern of soil nutrient availability in *Pinus canariensis* forests

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Abstract
• Soil resources are heterogeneously distributed in terrestrial plant communities. This heterogeneity is important because it determines the availability of local soil resources. A forest fire may change the spatial distribution of soil nutrients, affecting nutrition and survival of colonizing plants. However, specific information on the effects of ecosystem disturbance on the spatial distribution of soil resources is scarce.
• We hypothesized that, on a short-term basis, wildfire would change the spatial patterns of soil N and P availability. To test this hypothesis, we selected two *Pinus canariensis* forests burned in 2005 and 2000, respectively, and a third forest that was unburned since at least 1990 (unburned). We incubated ionic exchange membranes (IEMs) in replicated plots to estimate soil N and P availability and characterized the spatial pattern using SADIE (Spatial Analysis by Distance Indices).
• Mineral N, NO_3-N and PO_4-P availability, and aggregation and cluster indices for all nutrients were higher in the 2005 wildfire plots than in the 2000 wildfire and unburned plots.
• Our results suggest that surviving plants or new individuals becoming established in a burned area would find higher soil resources, but also higher small-scale heterogeneity in nutrients, which may have a major impact on the performance of individual plants and on the forest structure and dynamics.

Mots-clés :
feu de forêt /
membrane d'échange ionique /
SADIE /
disponibilité des éléments nutritifs du sol /
hétérogénéité spatiale

Résumé – Un incendie modifie la configuration spatiale de la disponibilité des éléments nutritifs dans les sols de forêts de *Pinus canariensis*.
• Les ressources du sol sont distribuées de manière hétérogène dans les communautés végétales terrestres. Cette hétérogénéité est importante car elle détermine la disponibilité locale des ressources du sol. Un feu de forêt peut changer la répartition spatiale des éléments nutritifs du sol, affectant la nutrition et la survie des plantes colonisatrices. Cependant, des informations précises sur les effets des perturbations des écosystèmes sur la répartition spatiale des ressources du sol sont rares.
• Nous avons émis l'hypothèse qu'à court terme, un feu de forêt pourrait modifier les modèles de répartition spatiale de disponibilité de N et P dans le sol. Pour tester cette hypothèse, nous avons sélectionné deux forêts de *Pinus canariensis* qui ont brûlé respectivement en 2005 et 2000, et une troisième forêt qui n'a brûlé depuis au moins 1990 (non brûlée). Nous avons incubé des membranes échangeuses d'ions (IEMs) dans plusieurs parcelles pour estimer la disponibilité du sol en N et P et nous avons caractérisé le modèle spatial en utilisant SADIE (Analyse spatiale en fonction d'indices de distance).
• N-minéral, N-NO_3, disponibilité en PO_4-P, agrégation et indices de cluster ont été plus élevés dans les parcelles incendiées en 2005 que dans celles incendiées en 2000 et les parcelles non brûlées.
• Nos résultats suggèrent que les plants survivants ou les plants en cours d'installation dans une zone brûlée, auront accès à des ressources plus abondantes, mais seront également confrontés à une hétérogénéité plus importante dans la disponibilité en éléments nutritifs. Cette dernière peut avoir un impact majeur sur la performance individuelle des plants et sur la structure et la dynamique forestières.

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1. INTRODUCTION

Spatial heterogeneity of essential plant resources on different spatial scales is ubiquitous in natural ecosystems (Gallardo, 2003; Guo et al., 2002; Jackson and Caldwell, 1993; Nicotra et al., 1999; Robertson and Gross, 1994; Robertson et al., 1997; Schlesinger et al., 1996). This spatial heterogeneity in the availability of soil resources can influence processes at the individual, population and community levels (Gallardo et al., 2006; Hutchings et al., 2003). Spatial variability in available soil nutrients may change during succession, or even within a single year, but patches of plant-available nutrients may reappear at the same spatial locations at irregular points in time (Cain et al., 1999; Gross et al., 1995; Guo et al., 2002; Ryel et al., 1996). The effect of disturbance on the spatial pattern of soil resources has been addressed by several authors. For example, disturbance by large herbivores increased the spatial pattern of soil N among sampling points separated by increasing distances from 5 to 30 m in a study by Augustine and Frank (2001). Schlesinger et al. (1996) also reported increasing spatial structure around individual plants with desertification, when grassland is replaced by shrubland. Hirobe et al. (2003) found increases in the spatial variability of nutrients over time since a fire, and Fraterrigo et al. (2005) found that land use has persistent, multi-decadal effects on the spatial heterogeneity of soil resources.

Fire is the most intense disturbance of nutrient cycling in temperate forest ecosystems (González et al., 2006; Grogan et al., 2000), with N being the most essential nutrient for plants and the most susceptible to losses after fire (Christensen, 1973). Several studies have tested fire impacts on soil resource availability (Carreira et al., 1994; DeLuca and Sala, 2006; Quintana et al., 2007; Romanya et al., 2001; Turner et al., 2007; Wienhold and Klemmedson, 1992). Ashes may provide an important source of available N after a forest fire on a short-term basis (Raison, 1979). However, on a long-term basis, recurrent fires may result in substantial losses of N from the forest ecosystem through volatilization and leaching from the soil, leading to lower N availability for plants (Vitousek and Howarth, 1991). For P, a similar temporal trend can be described, with higher availability after a forest fire followed by a decrease in total P and P availability on a long-term basis, possibly due to the decrease in organic P, lower phosphatase activity and lower mycorrhizal infection caused by wildfires (Alauzis et al., 2004).

In addition, ash distribution on the soil surface may play an important role in the spatial pattern of nutrient availability (Hirobe et al., 2003), with a great influence on plant colonization in ecosystems affected by fires (Grogan et al., 2000); however, this spatial dimension has not been well studied. Accordingly, the goal of this study was to describe the effect of wildfires on the spatial pattern of soil nutrient availability on a scale relevant for individual plants. We determined N and P availability because these nutrients frequently limit plant growth in forest ecosystems (Brahim et al., 1996; Vitousek and Howarth, 1991). We hypothesized that, on a short-term basis, wildfire would change the spatial patterns of soil N and P availability in *Pinus canariensis* forests. As a first possibility, if ashes deposited from burned organic matter are evenly distributed on the soil surface, the pre-fire spatial pattern may be less defined after the fire. As an alternative possibility, if ashes were deposited around (or intercepted by) surviving or dead individuals, a better-defined spatial pattern would be detected.

2. MATERIALS AND METHODS

2.1. Study area

The study was performed in three different *Pinus canariensis* Chr. Sm. ex DC. forests on the western face of La Palma Island (Canary Islands, Spain, 28^{o} 41' N, 17° 45' W). La Palma Island provides a unique opportunity to test the proposed working hypotheses because, in these forests, it is relatively easy to find plots with identical soil and site characteristics but burned in different years. Three characteristics make these forests unique. First, they are among the last natural and unmanaged pine forests of Europe. Second, far from the European continent and with low local N emissions, atmospheric N deposition is very low. Thus, nutrient deficiencies in trees are easily observed in pine needles, which increases the interest in nutrient cycling studies in these forests. Third, mature *P. canariensis* trees resist severe forest fires (Climent et al., 2004), burned stands being very comparable in terms of tree structure and age. The altitude of the study area is between 1200 and 1500 m, with mean annual rainfall of 600 mm and mean annual temperature of 16 °C (Climent et al., 2004). Soils are volcanic in origin, and are classified as Leptic Umbrisols (FAO, 1996). The soil organic matter content of the sampled plots ranged between 2 and 4%, with a soil pH between 6.5 and 7. The vegetation was dominated by the presence of *Pinus canariensis*, which accounted for 80% of the soil surface. Under the pine tree canopy, the understory was sparse and usually dominated by a single species, either *Adenocarpus viscosus* (Wild.) Webb & Berthel, *Erica arborea* L. or *Cistus symphytifolius* Lam.

2.2. Field sampling and lab analysis

Wildfires on the island were documented by the local environmental agency. These fires were intense and usually affected several hundred hectares. Fires in La Palma Island are restricted to the summer season. Although adult individuals of *Pinus canariensis* may lose all needles during a wildfire, most of them will regrow after the fire.

Three forests were selected for study in October 2006: two forests burned in 2005 and 2000, respectively, and a third that was unburned since at least 1990 (unburned). Using different sites in space in the place of a time series–a classic substitution in chronosequence studies–allowed us to study fire effects over a longer period of time than with a before/after fire approach. These forests were chosen because they were homogeneous in terms of altitude (see above), slope (less than 5%), basal area, pine age and understory vegetation. The regime of precipitation was also similar for all forests (see above). All forest fires were crown fires, and we found charcoal black stains along the pine bark. These stains occupied roughly the same pine bark surface and reached the same height in both the 2000 and 2005 forest fires. Therefore, fire intensities were likely similar across the forests. In each forest, plots were placed around three (2005 and 2000 wildfires) or four (unburned) randomly chosen individuals. Thus, in each plot there was at least one individual of the two more common plant

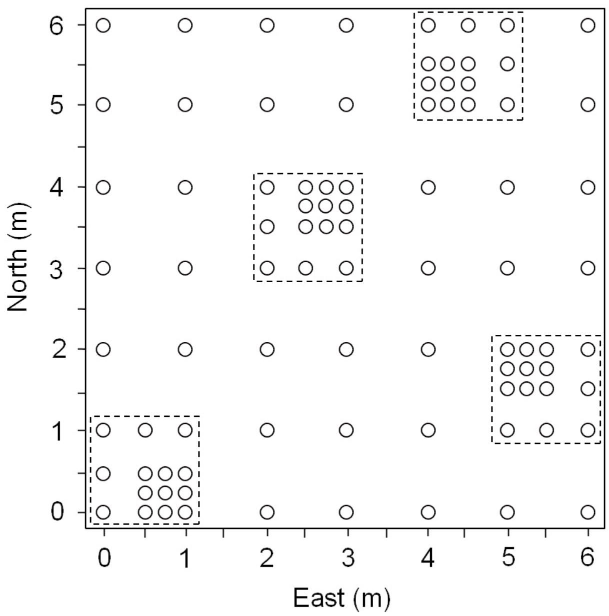

Figure 1. Sample design for a 6×6 m plot. Each circle shows a sampling point.

species (*Pinus canariensis* or *Adenocarpus viscosus*). Two *A. viscosus* and one *P. canariensis* individuals were selected for the 2005 and 2000 burned forests. For the unburned forest, two *A. viscosus* and two *P. canariensis* were sampled. Three plot sizes were selected (6×6, 4×4 and 3×3 m) depending on the size of the selected plant individual inside the plot. We aimed to detect the effect of the individual on the spatial properties with the maximum resolution possible. Thus, in the large plots (6×6 m) the sampling points were established every meter, but every half a meter in the smaller plots (4×4 and 3×3 m). In each plot, samples were taken on a finer scale, by randomly selecting four 1×1 m squares in the large plots and four 50×50 cm squares in the small plots. In each square, samples were taken at 25-cm intervals (large plots, Fig. 1) or 12.5-cm intervals (small plots). The total numbers of sampled points in the 2005, 2000 and unburned plots were 267, 299 and 420, respectively.

To estimate soil N and P availability, we used anionic and cationic exchange membranes (types I-100 and I-200, Electropure Excellion, Laguna Hills, California). The use of these ionic exchange membranes (IEMs) provides one of the most reliable indices of plant nutrient availability (Ziadi et al., 1999, 2000; Qian and Schoenau, 2002). IEMs simulate the flux of nutrients into roots (Huang and Schoenau, 1997). Compared with soil resource sampling methods commonly used (e.g., soil cores or buried resin-filled bags), the advantages of IEM spikes include inflicting minimal damage on the soil, being simple to use, and allowing intensive sampling over multiple time periods at the same spatial locations (Cain et al., 1999). Resin membranes were previously conditioned in the lab by immersing them in demineralized water at 82–90 °C for 48 h. After conditioning, 2.5×2.5 cm resin membranes were glued on a plastic holder to facilitate insertion into the soil. A plastic rod joined to the plastic holder helped to locate the resin membranes in the field. This design kept the membrane ionic exchange capacity unaltered (Cain et al., 1999). At each sampling point, anionic and cationic exchange membranes were incubated for 15 days at the end of September, a dry period of time. The membranes were positioned 5 cm below the top of the surface horizon with a metal spatula, and the soil around them was compacted to ensure good contact between the membranes and the soil. In lab conditions, replicate membranes inserted in soil samples yielded consistent results, with CV < 10%. Upon retrieval, the membranes were individually transported to the lab, air-dried, and cleaned of soil particles. We extracted NH_4^+, NO_3^- and PO_4^{3-} from the membranes by shaking them in 50 mL of 2 M KCl for 1 h at 200 rpm in an orbital shaker. These extracts were used to calculate the amount of NH_4-N and NO_3-N by colorimetry (indophenol blue method) using a microplate reader (Sims et al., 1995). PO_4-P concentration in the extract was determined by the molybdene blue method (Allen et al., 1986), and absorbance was measured with a microplate reader (D'Angelo et al., 2001). Mineral N was taken as the sum of NH_4-N and NO_3- N. Data were expressed as µg N dm^{-2} resin surface day^{-1}.

2.3. Statistical analysis

Approximative K-Sample Permutation Tests were performed to compare nutrient availability between plots burned in different years (Hollander and Wolfe, 1999). The exact p-values were approximated using Monte-Carlo resampling for all procedures (9999 permutations).

We used spatial analysis by distance indices (SADIE, Perry, 1998; Perry and Dixon, 2002; Perry et al., 1999) to characterize the spatial pattern of N and P availability. This method was originally developed for discrete variables; however, it can be successfully adapted for continuous variables by a previous categorization of these variables (Perry et al., 1999). Thus, we translate the value of each variable to the nearest integer, previously multiplying by 100 each of the variables to minimize the loss of information (Maestre and Quero, 2008). The SADIE technique consists of quantifying the spatial pattern in a sampled population by measuring the total distance that the individuals of the observed sample must move in order to reach a regular arrangement in space. Regularity corresponds to the situation where the sampled individuals are as dispersed as possible. Perry (1998) defined the index of aggregation (I_a). A value of $I_a > 1$ indicates the presence of an aggregated sample, an index equal to 1 characterizes a spatially random sample and a value of $I_a < 1$ indicates the presence of a regular sample. The index has an associated probability (P_a) that the data are not distributed randomly. This probability is obtained by comparing the observed spatial pattern with the corresponding values obtained by random permutations of the observed counts among the sample units.

Two standardized dimensionless cluster indices (ν_i and ν_j, Perry et al. 1999) were also used to provide a local measurement of the degree of small-scale clustering for each individual sample point. These indices quantify the degree to which the sampled count contributes toward clustering either as part of a patch or a gap. Clusters were defined as areas enclosed by contour levels of +1.5 or –1.5. When $\nu_i > 1.5$, the index indicates patchiness; when $\nu_j < -1.5$, it conveys the idea that the sampled point has membership of a gap, and when the cluster index equals 1, it indicates a random placement of that point value in relation to the others. To test the overall degree of clustering of the entire data, the mean values of the cluster indices, V_i and V_j respectively, were compared with corresponding values for randomizations in the same way as with I_a. Consequently, a map of the degree of clustering can help to visualize the areas where variable levels are relatively large or small. The cluster maps were made by

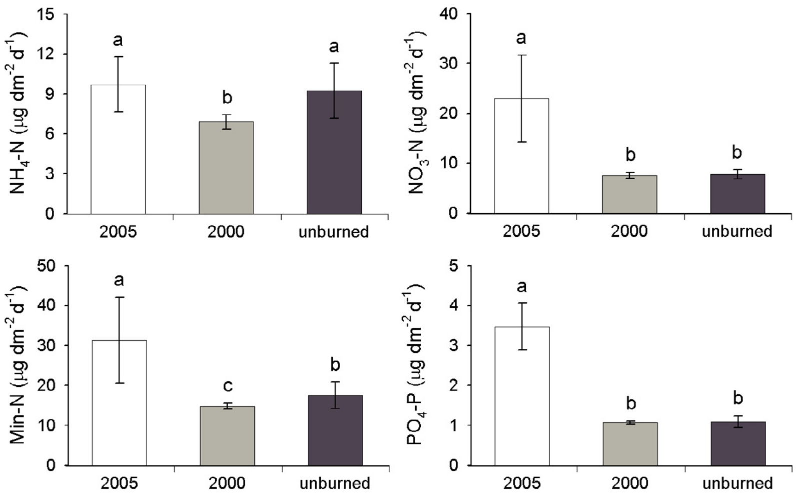

Figure 2. Soil nutrient availability (mean ± 2 SE) in plots burned during 2005 (n = 3), 2000 (n = 3), and unburned since at least 1990 (n = 4). Different letters denote significant differences ($p < 0.001$).

linear interpolation using the software Surfer 8.0 (Golden Software, Boulder, Colorado, USA).

Approximative K-Sample Permutation Tests were also used to compare SADIE indices between plots burned in different years, as described above. We first tested whether the time since the last wildfire affected the aggregation index distribution for nutrients, by permutation of the indices among wildfire years using the different nutrients (NH_4, NO_3 and PO_4 as blocks). Second, we analyzed each nutrient separately, obtaining an overall p. Post-hoc tests were performed for comparisons between wildfire years. All statistical analysis was performed using the Coin module in R 2.6.0 (R Development Core Team, 2007).

To test the effect of the extra pine plot in the unburned site, we sequentially removed each piece of pine plot data and performed the statistical analysis. No significant differences were found when either pine was removed from analysis, so we retained all sampled individuals in the unburned plot.

3. RESULTS

The time since the last wildfire showed significant effects on nutrient availability ($p < 0.001$). In the 2005 wildfire plots, NO_3-N, mineral N and PO_4-P availability were significantly higher than in the 2000 wildfire and the unburned plots (Fig. 2). However, NH_4-N availability in the 2005 wildfire plots was only significantly higher than in the 2000 wildfire plots. Soil NO_3-N availability was higher than NH_4-N availability in the 2005 wildfire plots, but both N forms showed similar values in the 2000 wildfire and the unburned plots (Fig. 2). Mean N-to-P availability ratios were 9.2, 14.9 and 18.3 in plots burned in 2005, 2000 and unburned plots, respectively.

The time since the last wildfire significantly affected the aggregation and cluster indices for all nutrients ($p < 0.05$). Most nutrients showed significant aggregated spatial patterns ($I_a > 1$, $p < 0.05$) in the 2005 wildfire plots. However, in the unburned plots, NH_4-N and mineral N showed a significant aggregated pattern in just one of the four plots, and NO_3-N and PO_4-P in two of the four plots. In plots burned in the 2000 wildfire, N forms showed significant aggregated patterns in two of the three plots, but PO_4-P showed random spatial patterns in all plots. For N forms, a significant decrease in mean I_a was observed from the 2005 wildfire to the unburned plots (Fig. 3). Similar results were observed for the cluster indices V_i and V_j. For PO_4-P, the highest I_a mean value was also observed in the 2005 wildfire, but significant differences were found only in comparison with the 2000 wildfire, where the lowest mean index was found. The cluster maps showed a decrease in the size and intensity of clusters and gaps from the 2005 wildfire to the unburned plots (Fig. 4).

4. DISCUSSION

As frequently found by other authors, soil N and P availability was associated with the time elapsed since the last wildfire. Soil NO_3-N and PO_4-P availability showed values approximately three times higher in the 2005 wildfire than in the 2000 wildfire or the unburned plots. This ephemeral increase in NO_3-N and PO_4-P availability is consistent with the literature (see Certini, 2005). Increases in the soil nitrification rate after fire have been related to increases in NH_4-N availability, soil temperature, water content and pH observed in burned soils (Raison, 1979).

In the 2000 burned plots, soil NH_4-N, NO_3-N and PO_4-P availability decreased significantly. Soil NO_3-N and PO_4-P availability showed similar low levels in the unburned plots: however, NH_4-N increased in these plots. This increase may be due to soil organic matter buildup since the last wildfire in these plots. This buildup in organic matter would enhance mineralization (Yermakov and Rothstein, 2006), increasing NH_4-N availability, but it apparently did not affect autotrophic nitrification or phosphate availability. Nitrification may depend on factors other than ammonium availability, and

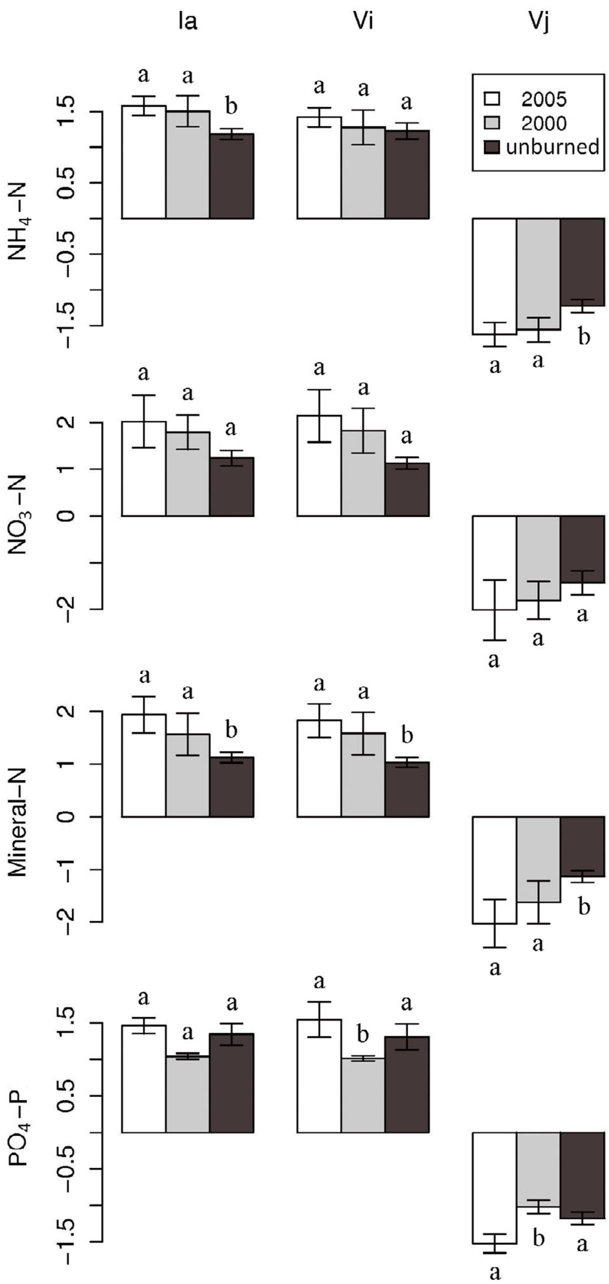

Figure 3. SADIE indices (mean ± 2 SE) for plots burned during 2005 (n = 3), 2000 (n = 3), and unburned since at least 1990 (n = 4). I_a = mean index of aggregation, V_i = mean index of clustering for patches, and V_j = mean index of clustering for gaps. Different letters denote significant differences between years ($p < 0.05$).

phosphate availability may be controlled through equilibrium with secondary soil minerals (Schlesinger, 1997).

We tested the hypothesis that ashes from burned organic matter would modify the spatial pattern of nutrient availability. As a first possibility, if ashes deposited from burned organic matter are evenly distributed on the soil surface, the pre-fire spatial pattern may be less defined. In this case, the index I_a would be the lowest just after a wildfire. As an alternative possibility, if ashes were deposited around (or intercepted by) surviving or dead individuals, a more intense spatial pattern would be detected, with the highest I_a in recently burned plots. Our results supported the latter possibility. For N, we detected a decrease in the mean I_a with the time elapsed since the last wildfire, although only differences between the 2005 wildfire and the unburned plots were statistically significant. Unlike N, P availability only showed a decrease in the mean aggregation index between the 2005 wildfire and the 2000 wildfire plots. In this paper, the highest definition of spatial patterns after fire suggested by the increase in aggregation indices may indicate the short-term effect of a disturbance on soil properties mediated by the presence of individual plants. N and P in the ash may be intercepted by large individual plants, or deposited beneath their canopies, which may increase the aggregation index in the most recently burned plots. Soil P availability after fire could be reduced more quickly than N by greater withdrawal through reactions with soil minerals (Smeck, 1985), which may explain the most rapid decline in the spatial pattern for this element. However, although we believe that this mechanism may well explain the differences between the different burned plots, caution is needed because our experimental design compared different plots in substitution for changes before and after fire. Thus, confounding factors other than fire are possible, and although the simplicity of *Pinus canariensis* forests in La Palma Island allowed us to discard the most obvious confounding factors, subtle differences in soil type may influence changes in the spatial pattern of nutrient availability.

Our results yielded different responses of soil N heterogeneity to fire than those reported by Hirobe et al. (2003). These authors observed an increased spatial variability with the time since the last fire in a dry tropical forest in Thailand, where wildfires occur almost annually without active fire prevention efforts. In contrast, the present paper focuses on the changes in soil nutrient availability with time since a single episodic fire, where fires are not so frequent. Fire frequency is one of the main factors conditioning the effect of fire on vegetation and soil dynamics (De las Heras et al., 2005).

Few studies have used IEMs in natural ecosystems, and comparisons with other studies are not as straightforward as with soil nutrient pools, because different resin membranes may differ in their capacity to absorb nutrients and full contact with soil particles may vary depending on soil type. However, we obtained values in the same range as those reported by Barret et al. (2002) in Antarctica. These low values may be because the membranes were incubated in the soil during a dry period with infrequent precipitation. Nutrient uptake by the membranes will depend on ion diffusion in the soil, which may be diminished in dry conditions (Subler et al., 1995). Low diffusion of ions in dry soils also affects root uptake, which makes resin membranes a good index of flow capacity and ion availability for plants in soils (Huang and Schoenau, 1997).

Our results suggested an increase in availability and aggregation patterns of soil N and P after fire. Thus, surviving plants or new individuals establishing on the burned area will find higher soil resources, but also higher small-scale heterogeneity, which can have a large impact on the performance of individual plants (Antonovics et al., 1987; Hutching et al., 2003;

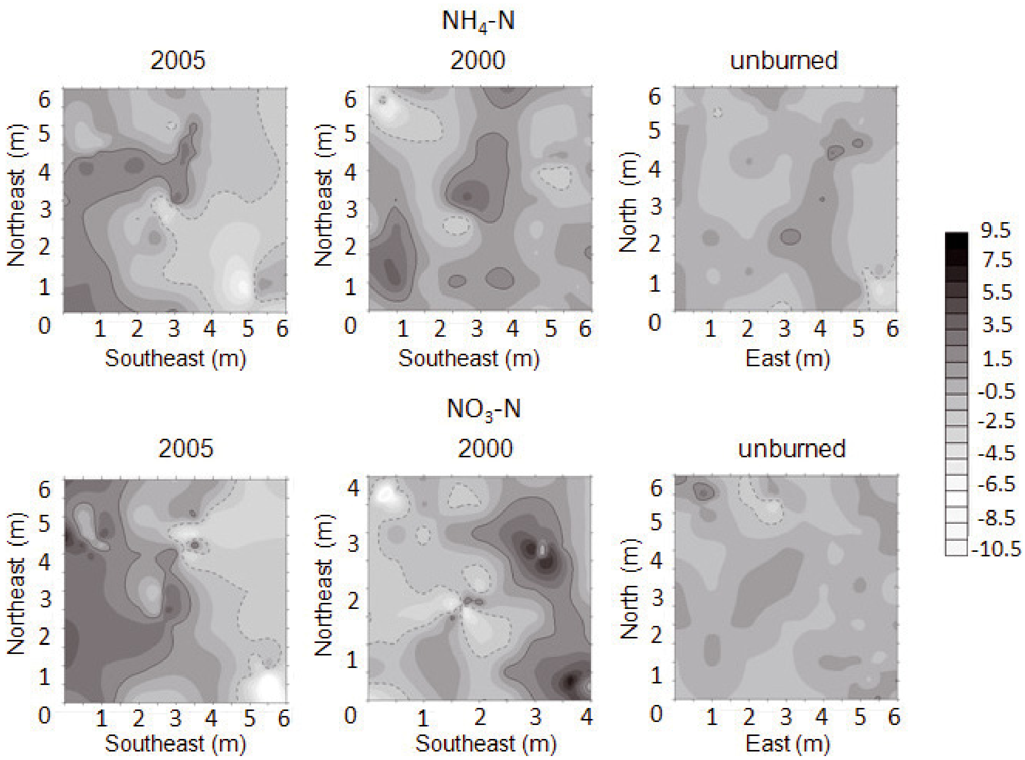

Figure 4. Cluster indices (v_i and v_j) for ammonium and nitrate availability for one replicate plot from each wildfire year. Solid lines show clusters of relatively high nutrient availability ($v_i > 1.5$). Dotted lines show clusters of relatively low nutrient availability ($v_j < -1.5$).

Miller et al., 1995), and therefore have an effect on the structure and dynamics of plant populations and communities.

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